

Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland

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Summary

1 Although outbreeding populations of many grassland plants exhibit substantial genetic and phenotypic variation at fine spatial scales (< 100 m²), the implications of local genetic diversity for community structure are poorly understood. Genetic diversity could contribute to local species diversity by mediating the effects of competition between species and by enhancing species persistence in the face of environmental variation.

2 We assayed the performance of three genotypes each of a dominant tussock grass (*Koeleria macrantha* [Ledeb.] J.A. Schultes) and dominant sedge (*Carex caryophyllea* Lat.) derived from a single 10 × 10 m quadrat within a limestone grassland in Derbyshire, UK. Genotypes were grown in monoculture and grass–sedge mixtures of different genetic composition in two environments of contrasting fertility. Species mixtures also included one genotype of the subordinate forb *Campanula rotundifolia* L.

3 When grown without neighbours, intraspecific genotypes responded similarly to environmental treatments. One genotype of the sedge performed worse in both environments than the other two sedge genotypes.

4 When grown in species mixtures, genotype performance was significantly influenced by the genetic identity of the neighbouring species for both the sedge and the grass. At high fertility, differential genotype performance was not sufficient to alter the expectation of competitive exclusion of the sedge by the grass. However, at low fertility, the competitive dominant depended on the genetic identity of both the grass and the sedge. In addition, each genotype of the grass performed best next to a different genotype of the sedge, and the identity of the best genotype pairings switched with environment.

5 Performance of a single genotype of the subordinate *Campanula* was not predictable by fertility alone, but by how fertility interacted with different neighbouring genotypes of both the grass and the sedge.

6 Results support the hypothesis that the genetic identity of interspecific neighbours influences plant performance in multispecies assemblages and mediates species' responses to environmental variation. Such interactions could be a key factor in the contribution of local intraspecific genetic diversity to species diversity.

Key-words: *Campanula rotundifolia*, *Carex caryophyllea*, genetic diversity, *Koeleria macrantha*, limestone grassland, species coexistence

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Introduction

Many plant populations exhibit significant, heritable phenotypic variation for a range of traits within very

small areas (Linhart & Grant 1996), including life-history characters (Linhart 1988; Argyres & Schmitt 1991), pathogen and herbivore resistance (Burdon 1987; Simms 1990), and growth allocation relating to resource capture and competitive ability (Turkington & Aarssen 1984; Turkington 1989). Although some fine-scale differentiation could be driven by genetic drift resulting

from very short dispersal or pollination distances (Argyres & Schmit 1991; Heywood 1991; Moody *et al.* 1993), it is widely believed that local genetic differentiation could be maintained by natural selection in response to fine-scale environmental heterogeneity in space or time (Wolf & Soltis 1992; Linhart & Grant 1996; Whitham *et al.* 2003). A significant component of such heterogeneity could be an individual's immediate biotic environment, such as neighbour identity (Linhart 1974, 1988; Turkington 1989). Despite limited evidence that perennial plants exhibit genotype-specific responses to competition that could be fine-tuned to the properties of their neighbours (Turkington 1979; Aarssen & Turkington 1985; Kelley & Clay 1987), the possibility of genetic processes influencing local species persistence and abundance remains a tantalizing prospect for connecting known patterns of local genetic diversity to community (Antonovics 1992; Booth & Grime 2003; Neuhauser *et al.* 2003; Vellend 2006) and ecosystem-level processes (Whitham *et al.* 2003; Crutsinger *et al.* 2006).

For most perennial plant communities, contributions of the local biotic environment to genetic differentiation remain poorly understood. An exception is the work of Turkington, Aarssen and others on *Trifolium repens*–*Lolium perenne* mixtures, which began with the demonstration by Turkington (1979) and Turkington & Harper (1979) that the performance of different genotypes of *Trifolium* varied in response to the biotic composition of their neighbourhoods. In a follow-up suite of experiments, Turkington & Aarssen (1984; see also Aarssen & Turkington 1985) further demonstrated that competition between *Lolium perenne* and *Trifolium repens* was more equitable between genotypes that exist as neighbours in the field, suggesting that natural selection favours more balanced competition between interspecific genotypes, and thus may contribute to species coexistence. Additional studies of the contribution of plant–microbial relationships to the success of genotype pairings of *Trifolium*–*Lolium* mixtures (Chanway *et al.* 1990; Luscher *et al.* 1992; Expert *et al.* 1997) have not undermined the basic recognition that these plants exhibit fine-scale adaptations to their local biotic environment (Turkington 1996). However, evidence for this phenomenon in other systems remains scarce (but see Kelley & Clay 1987; Taylor & Aarssen 1990; Vavrek 1998) and, until recently, was essentially unexplored for more natural, species-rich communities.

In a novel experimental investigation of whether the genetic composition of populations in a species-rich community contributes to community-level processes, Booth & Grime (2003) reported a stabilizing effect of genetic diversity on species composition. Using 16 clonal lines of each of 11 species sampled from a small area of limestone grassland in Cressbrookdale, Derbyshire, Booth and Grime demonstrated that communities maintained consistent composition across 10 replicates over 5 years if populations were represented by multiple

genotypes. Communities that were otherwise identical but contained a unique, single genotype for each species strongly diverged in composition after 5 years. Additional microsatellite-based assays of fifth-year genotype abundance in these microcosms by Whitlock and colleagues (Whitlock 2004; Whitlock *et al.* in press) suggest effects of genetic diversity were driven largely by performance differences between intraspecific genotypes. However, the existence of 'good' and 'bad' genotypes under the constant environmental conditions of the Booth and Grime study does not explain the origin or maintenance of considerable levels of local genetic and phenotypic differentiation uncovered in the Cressbrookdale ecosystem, nor does the randomized placement of individuals in the Booth and Grime design allow for direct tests of genotype-mediated interactions between species. In particular, the absence of environmental variation in this study suggests additional research is needed to determine whether the role of genetic diversity in multispecies communities is contingent upon sufficient heterogeneity in the local environment. Such heterogeneity, particularly in the form of grazing intensity and the physical and chemical properties of the substrate, has been shown to be an important driver of species-level vegetation structure at Cressbrookdale (Pearce 1987) and Carboniferous Limestone grasslands in general (Balme 1953; Pigott 1962).

To test whether the performance of genotypes of selected species from the Cressbrookdale ecosystem differs with respect to the genetic identity of neighbours, and also whether such competitive responses shift depending on the nature of the environment, we conducted a pairwise competition study of selected genotypes of three species from the Booth and Grime microcosms. We were particularly interested in (i) whether some sampled genotypes from Cressbrookdale exhibit adaptations to a different but relatively frequent micro-environment of sheep and cattle dung patches, which experience high rates of nutrient supply and low to non-existent rates of grazing for extended periods; (ii) whether such adaptations would be apparent for individuals grown alone vs. those grown in close proximity to a common interspecific neighbour; and (iii) whether the genetic identity of the neighbour influences the outcome of the above two processes. Our experimental design included three genotypes each of a dominant grass, the tussock species *Koeleria macrantha*, and a locally abundant sedge, *Carex caryophyllea*, grown in monoculture and all nine interspecific pairwise combinations; these compositions were subjected to two environments representing the grazed, oligotrophic environment of the Booth and Grime study and the more fertile, ungrazed environment of dung patches. To explore further the consequences of genetic identity of a dominant species on the performance of a common but subordinate species, we also measured the performance of one genotype of the small forb *Campanula rotundifolia* in the *Koeleria*–*Carex* mixtures.

Methods

Three genotypes of *Carex caryophylla* and *Koeleria macrantha* and one genotype of *Campanula rotundifolia* were selected from 16 clonal lines of each species established at Tapton Experimental Garden, University of Sheffield, UK, in 1995 by R. Booth and J. P. Grime (Booth & Grime 2003). All clones were obtained by random sampling within a 10 × 10 m area of ancient species-rich calcareous grassland at Cressbrookdale in North Derbyshire, UK, with subsequent clonal propagation at Tapton. Three genotypes of *Carex* (Cc4, Cc9, Cc13) and *Koeleria* (Km13, Km3, Km4) were selected to represent the range of abundance of the initial 16 genotypes after 5 years in simulated single-genotype microcosms as reported in Booth & Grime (2003). Selection of the *Campanula* genotype (Cr13) was based upon its potential for clonal spread. Whitlock (2004), using microsatellite markers, has established the genetic uniqueness of each of these clones. Year-round weeding and flower removal since clonal lines began has prevented sexual diversification and invasion by ambient genotypes.

One hundred and twenty-eight 18-cm-diameter × 20-cm-deep pots were filled with infertile rendzina soil removed from the field (top 30 cm) at a nearby limestone grassland site (Harpur Hill, Derbyshire) chosen to match substrate conditions at Cressbrookdale. Pots receiving species mixtures were each planted with five individuals representing three species: one individual of *Campanula* in the pot centre, two individuals of the same *Carex* genotype (on either side of the pot centre midway along the pot radius) and two individuals of a *Koeleria* genotype (along an axis perpendicular to *Carex* individuals). In each pot a species was represented by one genotype. Monoculture pots received only two individuals of either *Carex* or *Koeleria* planted in the same positions as for mixtures. Individuals were transplanted in January 2005 and remained in glasshouse conditions to promote establishment until March 2005, when they were placed outdoors in four randomized blocks at Tapton Experimental Garden until harvest. High-fertility pots received 1.56 g 20 : 10 : 10 NPK fertilizer in June 2005, were not clipped and were wrapped with clear plastic collars to prevent spillover of growing leaves. Low-fertility plots did not receive fertilizer and were clipped to 2.5 cm height in July 2005, October 2005 and July 2006. All 128 pots were harvested at soil level in early October 2006, and above-ground biomass was separated by species and dried to constant mass.

Statistical analyses of above-ground biomass per pot were separated into monoculture (56 pots) and mixture (72 pots) components. Performance of monocultures of *Carex* and *Koeleria* were tested by ANOVA with respect to block, target genotype, fertility level and a genotype–fertility interaction. Mixture performance of all three species was tested with species-specific ANOVA models with respect to block and single-factor and two- and three-way interaction terms of target genotype, neighbour

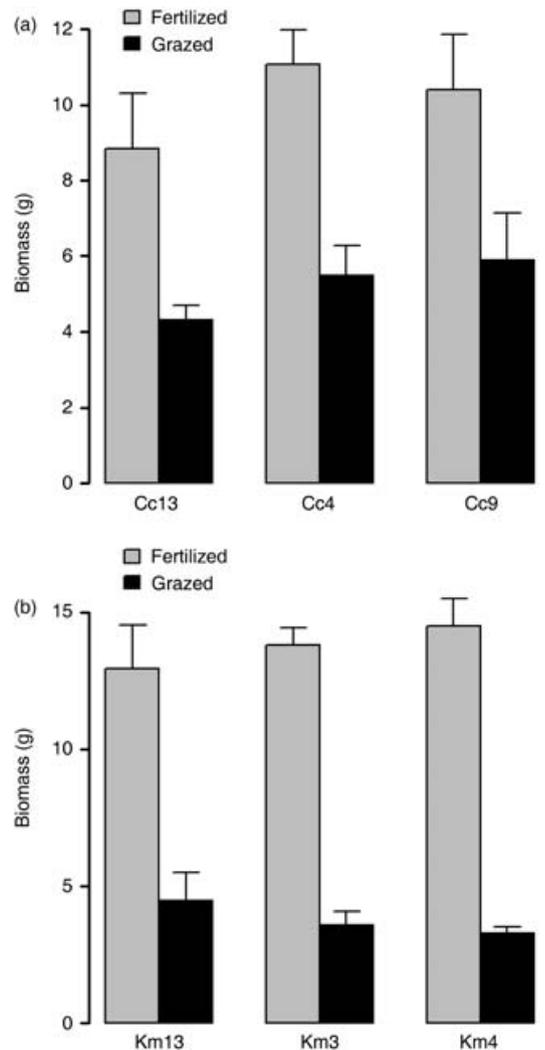


Fig. 1 Above-ground biomass (g) per pot (two individuals) of three genotypes of (a) *Carex caryophylla* and (b) *Koeleria macrantha*, grown in monoculture under two fertility levels. Error bars indicate 1 SE, $n = 4$.

genotype and fertility level (*Campanula* models did not include the target genotype term). Model residuals were checked for normality but no transformations were required.

Results

Carex and *Koeleria* genotypes were strongly influenced by environmental treatment in monoculture, with *Carex* genotypes producing double and *Koeleria* genotypes nearly triple the biomass in high-fertility, ungrazed pots (Fig. 1a,b; fertility effect $P < 0.001$, both species). *Carex* genotype Cc13 produced significantly less biomass than Cc4 or Cc9, regardless of fertility level ($P < 0.05$), but genotypes of *Koeleria* performed equally ($P > 0.1$). No genotype–fertility interactions were detected but performance of both species varied by block (*Carex* model block effect $P < 0.001$, *Koeleria* $P < 0.05$). Models for both species explained nearly all variation in monoculture performance ($R^2 > 93\%$).

Table 1 ANOVA results of models describing performance in mixture of three genotypes of *Carex caryophylla* (top) and three genotypes of *Koeleria macrantha* (bottom) in response to block, target and neighbour genotype ('Cc' or 'Km'), environmental treatment (Fertility), and all two- and three-way interactions. ANOVA R^2 values were 0.53 and 0.92 for *Carex* and *Koeleria* models, respectively

Factor	d.f.	SS	MS	F	P
Target: <i>Carex caryophylla</i>					
Block	3	6.27	2.09	2.31	
Cc genotype	2	3.90	1.95	2.15	
Km genotype	2	20.88	10.44	11.53	***
Fertility	1	0.16	0.16	0.17	
Cc:Fertility	2	6.18	3.09	3.41	*
Km:Fertility	2	7.58	3.79	4.18	*
Cc:Km	4	5.07	1.27	1.40	
Cc:Km:Fertility	4	2.55	0.64	0.70	
Residuals	51	46.17	0.91		
Target: <i>Koeleria macrantha</i>					
Block	3	39.14	13.05	7.47	***
Cc genotype	2	9.10	4.55	2.61	
Km genotype	2	11.78	5.89	3.37	*
Fertility	1	943.52	943.52	540.44	***
Cc:Fertility	2	6.46	3.23	1.85	
Km:Fertility	2	14.55	7.27	4.17	*
Cc:Km	4	18.43	4.61	2.64	*
Cc:Km:Fertility	4	21.93	5.48	3.14	*
Residuals	51	89.04	1.75		

*** $P < 0.001$; * $P < 0.05$.

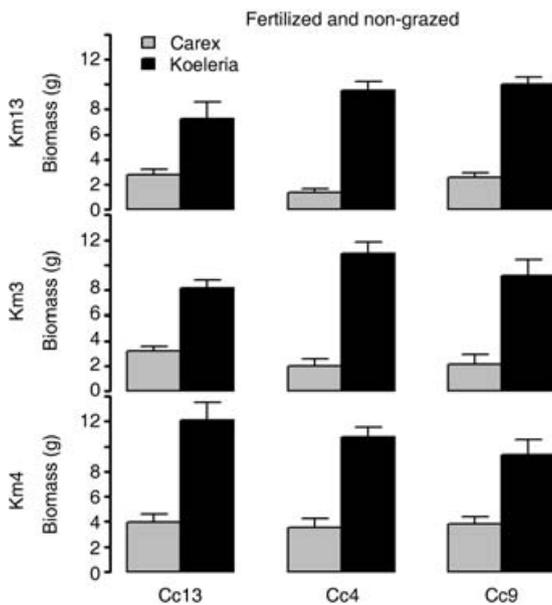


Fig. 2 Above-ground biomass (g) per pot (two individuals) of *Carex caryophylla* (grey bars) and *Koeleria macrantha* (black bars) genotypes in pairwise, interspecific mixtures at high fertility in the absence of grazing. Error bars indicate 1 SE, $n = 4$.

When grown in mixture with *Koeleria* and *Campanula*, neither fertility alone nor *Carex* genotype alone predicted *Carex* performance. Instead, the largest effect on *Carex* performance was the genetic identity of its

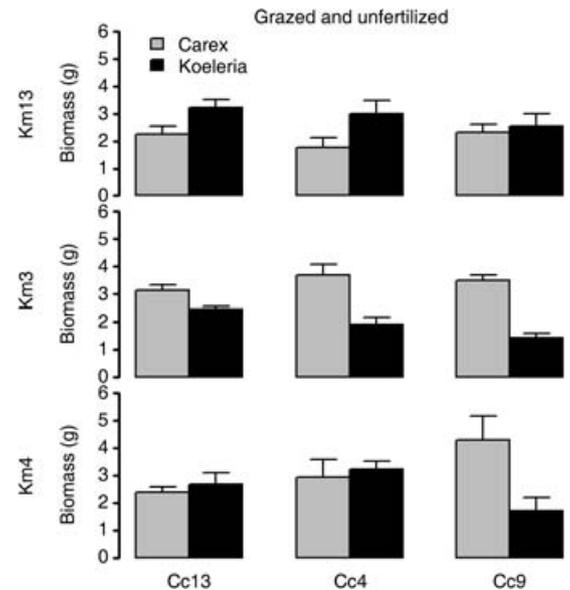


Fig. 3 Above-ground biomass (g) per pot (two individuals) of *Carex caryophylla* (grey bars) and *Koeleria macrantha* (black bars) genotypes in pairwise, interspecific mixtures under low fertility and simulated grazing. Error bars indicate 1 SE, $n = 4$.

Koeleria neighbour, an effect that varied significantly with fertility (Table 1). There was a minor but significant interaction between *Carex* genotype and fertility (Table 1). In the high-fertility, ungrazed environment, all *Carex* genotypes were significantly suppressed by all *Koeleria* genotypes (Fig. 2). However, in the low-fertility environment, *Carex* was dominant in four of the nine mixtures, and in three of the remaining cases was nearly equivalent in performance to *Koeleria* (Fig. 3). All *Carex* genotypes were dominant when competing against genotype Km3, and genotype Cc9 was dominant over all but one *Koeleria* genotype (Fig. 3).

Mixture performance of *Koeleria* was significantly enhanced by high fertility regardless of *Carex* neighbour identity (partial $R^2 = 0.82$, Table 1), with Km4 outperforming the other two genotypes ($P < 0.001$). However, *Koeleria* performance depended in part on the three-way interaction of Km genotype, Cc genotype and fertility (Table 1), presenting a complex set of relationships between the two species and their environment. Under high fertility, Km13 produced the most biomass when grown with Cc9, Km4 with Cc13 and Km3 performed best with Cc4 (Fig. 2). Under low fertility, Km13 switched to best performance under Cc13, Km4 switched to Cc4 and Km3 switched to Cc13 (Fig. 3). *Koeleria* was dominant at high fertility regardless of its genetic identity and that of its neighbour. At low fertility, however, only Km13 was consistently dominant (Fig. 3).

Performance of the subordinate forb *Campanula rotundifolia* amidst *Carex* and *Koeleria* neighbours was highly variable (Fig. 4) and not predictable by fertility treatment alone ($P > 0.5$), but depended significantly on interactions between both neighbour species and fertility ($P < 0.05$ for both *Koeleria* and *Carex* genotype effects).

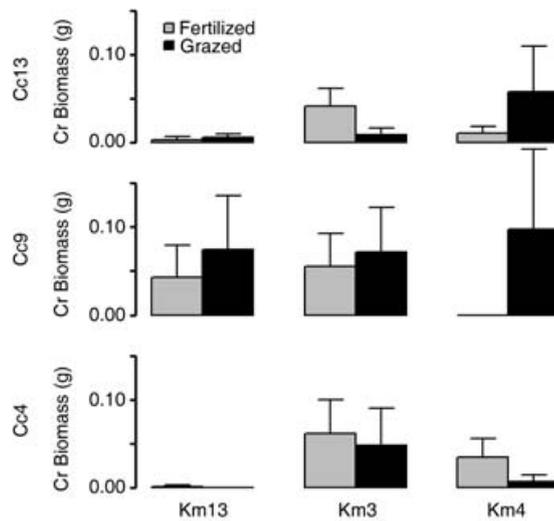


Fig. 4 Above-ground biomass (g) per pot (two individuals) of one genotype of *Campanula rotundifolia*, grown under two fertility levels and with different genotypes of two neighbours, *Carex caryophylla* (Cc) and *Koeleria macrantha* (Km). Error bars indicate 1 SE, $n = 4$.

Discussion

In what remains the only study of its kind, Booth & Grime (2003) demonstrated a relationship between compositional stability in a community of 11 species and the genetic diversity of component populations, all sampled from within a 10×10 m area in the limestone grassland at Cressbrookdale, Derbyshire. By assaying the performance of selected genotypes of three species in the Booth and Grime experiment in response to neighbours of varied genetic identity in different environments, the present study helps define the mechanisms that underlie the sensitivity of communities to genetic impoverishment and that promote and maintain such levels of genetic diversity at Cressbrookdale. In line with past and current theory (Antonovics 1978; Aarssen 1989; Vellend & Geber 2005; Vellend 2006), our study suggests local genetic diversity influences species coexistence and community composition in two complementary ways.

First, genotype–environment interactions, in which genotypes are best adapted to different environmental conditions, can buffer extinction risk in the face of local environmental heterogeneity (Williams 1975; Aarssen 1992; Vellend & Geber 2005). Our experiment does not offer support for this process when only monoculture genotype performance is considered (Fig. 1). However, in the presence of neighbours, significant interactions of target genotype and fertility were detected for both *Carex* and *Koeleria* (Table 1), suggesting that local substrate variation could be a significant driver of the relationship between local genetic diversity and species diversity at Cressbrookdale. Aarssen (1992) suggested that the presence of genotype–environment interactions at the genotype level can lead to complex interaction

networks in which species coexistence is the rule rather than the exception. By revealing genotype–environment interactions in mixture only, our study highlights the potential complexity involved in modelling species interactions in an environment that offers considerable fine-scale variation in both abiotic (substrate) and biotic (grazing intensity) factors, even when modelling only a small subset of the species involved.

Second, even in the absence of environmental variation, genetic diversity itself may promote competitive equivalence between species if the outcome of competition depends on the genetic identity of competing species (Aarssen 1989, 1992, 2005; Vellend & Geber 2005; Vellend 2006). For example, genetic diversity can have a stabilizing effect (*sensu* Chesson 2000) on coexistence if it results in intransitive competitive relationships at the species level, where no single species is competitively dominant (Gilpin 1975; Aarssen 1989; Taylor & Aarssen 1990; Laird & Schamp 2006). Intransitivities at the genotype level could also have an equalizing effect on species interactions, where genetic diversity acts to slow competitive exclusion (Laird & Schamp 2006). When combined with continual biomass removal and slow growth dynamics created by the infertile substrate, intransitivities like those apparent in Fig. 3 can essentially render the process of competitive exclusion to the same time scale as long-term environmental variation, making the concept of stable coexistence irrelevant to extant patterns of species diversity (Aarssen 1992). In a more fertile, undisturbed environment, our results suggest *Koeleria* would quickly displace *Carex* (Fig. 2), regardless of genetic diversity. In the typical grazed, oligotrophic conditions of Cressbrookdale, however, our results suggest that genetic diversity acts to mediate competitive relationships at the species level (Fig. 3). Thus, our results most strongly support a ‘slow dynamics’ model of species coexistence at Cressbrookdale in which competitive exclusion, long-term environmental variation and even speciation occur on similar time scales (Aarssen 1989; Hubbell 2001).

Part of the motivation for our experiment was the experimental demonstration by Booth & Grime (2003) that communities of more genetically diverse populations exhibit greater compositional stability at the species level. Using molecular markers to identify the fate of genotypes after 5 years in the Booth and Grime experiment, Whitlock *et al.* (in press) evaluated two alternative hypotheses underlying the Booth and Grime result, relating to whether the relative abundance of intraspecific genotypes was consistent among genetic diversity treatments. The finding of Whitlock *et al.* that genotype abundances of most species were correlated among genetic diversity treatments suggests that the constant microcosm environment, to a major extent, selected for genotypes of innate ability to tolerate canopy removal and low fertility, regardless of neighbour identity and complexity. However, the results we present here do not support this strict interpretation for all species in the Booth and Grime experiment. Instead, we demonstrate

that, even under the constant conditions of our pot experiment, pairwise interactions at the species level can depend strongly on the genetic identity of the competitors and can shift competitive outcomes at the species level (Fig. 3). Importantly, although the abundances of particular *Carex caryophyllea* genotypes were correlated across genetic diversity treatments in the Booth and Grime microcosms, those of *Koeleria macrantha* were not (Whitlock 2004; Whitlock *et al.* in press). From this suite of investigations of the role of local genetic diversity in community-level processes in the Cressbrookdale ecosystem, what seems clear is that genetic diversity may act as a buffer to local species extinction through both (i) the provision of robust genotypes for a particular environmental condition (particularly when in competition, as discussed above), and (ii) serving as a significant source of intransitivity between species. These processes are not mutually exclusive, and their relative importance will depend on a potentially large suite of both biotic (degree of local genetic differentiation) and abiotic (degree of local heterogeneity) factors, which vary by species and location.

The considerable influence of neighbour genetic identity on target genotype performance in both environments in our study creates the opportunity for significant coevolution and local adaptation in the Cressbrookdale ecosystem, echoing results from other studies in which attributes of individuals have been found to be finely adapted to neighbouring competitors or pests (Callaway & Aschehoug 2000; Ehlers & Thompson 2004; Callaway *et al.* 2005; Thompson 2005). Maintenance of genetic diversity is likely to be influenced by the diverse array of neighbours at Cressbrookdale; however, local biotic complexity itself works against finely tuned adaptations to specific neighbouring individuals, given 30 or more species can be present within 1 m². Pairwise coevolution between individuals may thus be less apparent at Cressbrookdale than in other recently described systems (e.g. Ehlers & Thompson 2004).

Performance of a single genotype of the subordinate species *Campanula rotundifolia* varied strongly with respect to the genetic identities of its dominant neighbours (Fig. 4), and not consistently between fertility levels. Local genetic diversity of dominant species should thus provide a significant selection pressure for *Campanula* at Cressbrookdale, and in turn could generate considerable genetic diversity in local *Campanula* populations, supporting a 'diversity begets diversity' model of genetic diversity (Whittaker 1975; Palmer & Maurer 1997; Vellend & Geber 2005). Although *Campanula* has a well-known ability to alter its morphology in relation to both above-ground and below-ground competition (Campbell *et al.* 1991), the contribution of genetic differences to this behaviour is not well understood. However, *Campanula* does exhibit significant local genetic differentiation at Cressbrookdale (Whitlock 2004).

We suggest it is no coincidence that the few existing empirical demonstrations of high fine-scale genetic diversity and its relationship to community-level processes come from grazed or mown ecosystems (Turkington & Harper 1979; Turkington 1979; Aarssen & Turkington 1985; Kelley & Clay 1987; Vavrek 1998), and that much of the world's most species-rich vegetation at fine scales is associated with both regular disturbance (grazing, recurrent drought or fire) and infertile soils (Fridley *et al.* 2006). If mediation of competitive relationships is both a consequence and a potential cause of local genetic diversity (Vellend & Geber 2005), then local genetic and species diversity should be correlated (Vellend 2003) and both a response of vegetation to environments in which competitive superiority is not directly related to plant size due to the uncoupling of apical dominance and fitness in such habitats. As Aarssen (1989, 2005) has suggested for plants in general, and Herben *et al.* (2001) have emphasized specifically for disturbed, oligotrophic environments, there should be more ways to be a good competitor if vertical size does not contribute to competitive ability. Reduced selection pressure on size-related traits should favour the establishment and persistence of myriad intraspecific genotypes, which in turn should greatly slow competitive relationships among species. We thus suggest that ecosystems in which the importance of apical growth is diminished from recurrent disturbance and slow growth dynamics, like Cressbrookdale, should consistently exhibit high levels of genetic and species diversity, regardless of underlying environmental heterogeneity. Furthermore, resource addition and removal of disturbance should undermine both genetic and species diversity by focusing local genetic selection on the single strategy of fast apical growth (Grime 2001).

Conservation and restoration of grassland communities can be hampered by insufficient consideration of the genetic composition of existing or sown populations (Knapp & Rice 1996; Hufford & Mazer 2003). The relevance of genetics in these circumstances is often viewed as one of local adaptation to particular environmental or biotic conditions (Oldfield 1984). Although this is clearly an important consideration, our study further suggests that 'getting the right genotype' must be viewed in concert with an approach that explicitly considers fine-scale genetic diversity as an equalizing mechanism preventing local extinction. For example, a grazed community on infertile substrate planted with each of the three genotypes of *Koeleria* and *Carex* in our study would be expected to exhibit species coexistence for some time (Fig. 3). Genetic impoverishment in the form of removal of a single genotype of each species (Km3 and Cc9) should lead to rapid dominance by *Koeleria*, thus providing clear management implications of local genetic diversity. Although such dynamics will always depend on the genetic differentiation of the species involved, the planting or conservation of many local genotypes should have important pragmatic implications for species coexistence in grassland systems.

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